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100 Years of Consolidation— Remembering Müller and Pilzecker

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Introduction

The origin of the concept of memory consolidation and the introduction of the term “consolidierung” (consolidation) to the modern science of memory are generally credited to Georg Elias Müller (1850–1934), professor at the University of Göttingen, Germany, and his student Alfons Pilzecker. Their seminal monograph “Experimentelle Beiträge zur Lehre vom Gedächtnis” (Experimental Contributions to the Science of Memory), published in 1900, proposed that learning does not induce instantaneous, permanent memories but that memory takes time to be fixed (or consolidated). Consequently, memory remains vulnerable to disruption for a period of time after learning.

Georg Müller was among the founders of experimental psychology. Inspired by the work of Gustav Fechner (1801–1887), Wilhelm Wundt (1832–1920), and Herman Ebbinghaus (1859–1909),¹ he was an early advocate of the view that mental function results from the action of matter, and that learning and memory should thus exhibit lawful properties. In their 300-page monograph, Müller and Pilzecker reported 40 experiments, carried out between 1892 and 1900, which were designed to identify the laws that govern memory formation and retrieval. Although Müller and Pilzecker have been frequently acknowledged for introducing the concept of memory consolidation,² their monograph has not been translated and knowledge of their methods and experimental findings has faded with the passing of almost a century. This commentary is intended to outline the experimental work of Müller and Pilzecker to explicate how the concept of memory consolidation originated.³

In their studies, Müller and Pilzecker used lists of nonsense syllables, which had been introduced by Ebbinghaus (1885). In his experiments, Ebbinghaus determined the number of trials that were needed to reproduce all of the syllables in a studied list twice without error (method of complete mastery). The methods of Müller and Pilzecker differed in

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¹For biographical sketches and bibliographies, see Boring (1950).

²The Science Citation Index lists 46 citations since 1955.

³Earlier discussions of Müller and Pilzecker can also be found in McDougall (1901); Glickman (1961); and McGaugh and Herz (1972).

three ways. First, they trained their subjects using nonsense syllables that were presented as paired associates. Lists were read aloud with emphasis on every odd-numbered syllable, thus creating pairs of emphasized and nonemphasized syllables, or trochees. To test memory, volunteers were cued with the first syllable of each pair, in a mixed order, and asked to recall the second syllable of the pair. Thus, if the list A-b-C-d-E-f were used for training (where each uppercase letter denotes the emphasized syllable of a pair), the correct answers to the cue syllables E, A, C would be the syllables f, b, and d. This novel procedure had originally been developed in Müller's laboratory by Jost (1897). Second, instead of counting the number of trials necessary to reproduce the paired associates correctly, Müller and Pilzecker fixed the number of training trials and quantified memory by determining the percentage of correctly recalled syllables, the percentage of incorrect answers, and the percentage of recall failures. This method is in such common use today that it is not often appreciated as an experimental innovation. Third, they constructed a sophisticated apparatus for determining the response latency for recall (see Appendix for details).

The Beginnings of Consolidation Theory

The line of evidence that would eventually result in the concept of memory consolidation began with a simple observation. Volunteers for the experiments of Müller and Pilzecker occasionally reported a strong tendency for syllable pairs to come to mind repeatedly between training sessions, despite efforts to suppress this intrusion. Müller and Pilzecker adopted the German word "perseveration" (p. 60) from descriptions of psychiatric illness to refer to this benign phenomenon. Pursuing the reports of their volunteers, they found evidence for perseveration during recall testing itself. For example, some individuals, recalled a syllable correctly in response to its proper cue but, in subsequent tests, continued to use the same syllable incorrectly in response to another cue (experiment 26). Also, incorrectly recalled syllables often belonged to the list that contained the correct syllable rather than being simply unrelated to previously trained material. This effect was strongest immediately after training, decayed during the subsequent minutes, and was not present after 1 day (Fig. 1; experiments 5, 7, 15, and 29). Müller and Pilzecker concluded that these peculiar mistakes resulted from the perseveration of recently learned material. Moreover, they speculated that perseveration was the result of transient activity in the brain that encoded the associative memory and suggested that this activity functioned as a short-term form of memory, similar to the primary memory proposed by William James (1842–1910).

The sequence of our thoughts . . . is often interrupted by external or internal disruptions. Were it not for a spontaneous tendency of these thoughts to regain conscious awareness after a perturbation, such disturbances would prevent the completion of important trains of thought. (p. 75)

Importantly, Müller and Pilzecker suggested that the perseveration of syllable pairs might be necessary not only for establishing representations of the syllables in memory but for strengthening the associations between them. If so, they argued, disrupting perseveration should interfere with the formation of associative learning.

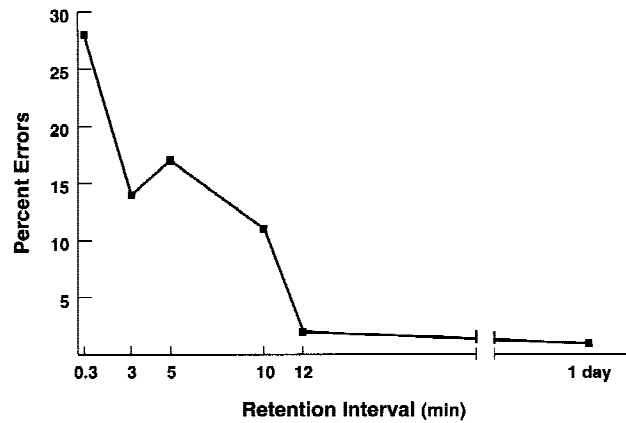


Figure 1: Evidence for perseveration. Subjects were tested for retention of paired syllables at various intervals after learning by cueing them with the first syllable of each pair. Incorrect answers were divided into syllables that belonged to the same list as the cue syllable (list correct errors) and syllables that did not belong to the studied list. Plotted here is a subset of list correct errors, in which the incorrectly recalled syllable belonged to the cue of the immediately preceding pair in the study list. The percentage of these errors decreased rapidly for ~10 min following learning. This observation was interpreted as evidence for the perseveration of the studied syllables for ~10 min. (From data reported on p. 65; experiments 5, 7, 15, and 29).

The experience of everyday life shows that perseverative tendencies of different parts of a train of thought can be weakened considerably by turning one's attention with energy to a different matter. . . . One can question, however, whether the effect of such an intense mental occupation . . . , immediately following reading of a list, simply reduces the frequency with which syllables of this list spontaneously regain conscious awareness. One might deem that the perseverative tendencies of syllables of a previously read list might also serve to consolidate the associations between these syllables . . . and that accordingly, weakening of the perseverative tendencies of syllables from a previously read list, due to other intense mental occupations, might have the additional effect of obstructing the associations between these syllables. (p. 68)

The Discovery of Retroactive Inhibition

Müller and Pilzecker designed 10 experiments to test the hypothesis that perseveration reflected an internal, physiological process that serves to strengthen associative memories. Three representative experiments are described here. In experiment 31 (Fig. 2), a volunteer received eight training trials with six pairs of syllables (list A), which took ~1 min. After an interval of 34 sec a second list (list X) was read eight times to prevent the perseveration of syllables from list A. Then, after a longer interval of 6 min, cue syllables from both lists A and X were presented in mixed order, and the percentage of correctly recalled syllables from list A was determined. To examine the effect of the interpolation of list X on recall of list A, a third list (list B) was trained eight times and recall was tested after an equivalent interval, but without interpolated learning. Retention of associations from list A was lower than retention from list B (23% vs.

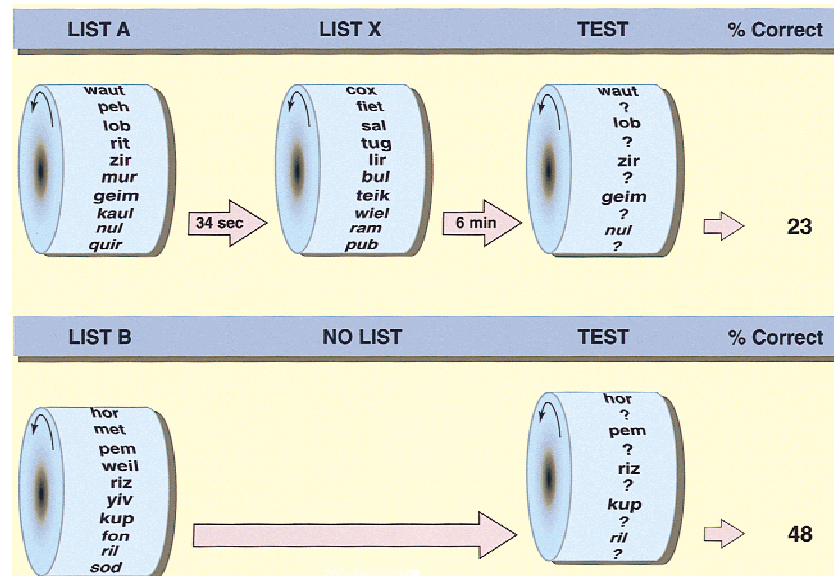


Figure 2: Retroactive inhibition of verbal material. Lists of 12 syllables were mounted on rotating drums and read aloud as pairs by emphasizing every other syllable. A subject was given eight training trials with syllable pairs from list A (total training time, ~1 min) followed by eight training trials with an interpolated list X. Retention was then tested 6 min after studying list X and compared to retention of a third list B, which was tested without an interfering list. Retention of list A was poorer than retention of list B, suggesting a retroactive inhibition of list X on the associations from list A. (From data reported on p. 181; experiment 31).

48%), suggesting that the interpolation of list X had interfered with memory for the associations from list A. Similar results were obtained when the interval between list A and X was 1 min, and the retention interval was 24 hr. Müller and Pilzecker commented:

The suspicion imposed on us by these results was that the processes that serve the formation of associations in a list of syllables continue for some time after reading of the list, but that they would be weakened by another intense mental occupation, such that an intense mental occupation following reading of a list of syllables would inhibit associations of that list. Because this type of inhibition acts on the effect of an ostensibly completed process ... we will call it ... "retroactive inhibition." (p. 179)

In another study (experiment 34), Müller and Pilzecker determined that retention (measured at 1.5 hr) of the first of two lists was impaired if the second list followed after a brief interval of 17 sec but was not affected when the second list followed after a longer interval of 6 min. This experiment suggested

... that the associations of a [list] of syllables are being inhibited less by a subsequently read list, the later the [interpolated list] is being read. [This is] because the longer the

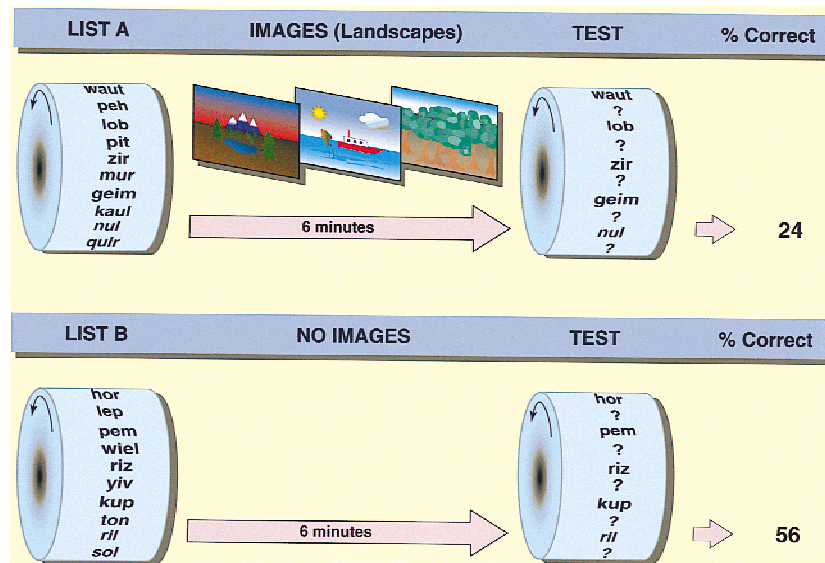


Figure 3: Retroactive inhibition by pictorial material. Syllables from list A were trained and followed immediately by a 6-min presentation of three painted landscapes. The subject was asked to describe the pictures. Retention of list A was then compared to retention of a control list B. The result suggested that even material not related to what had been studied could interfere with retention. (From data reported on p. 188; experiment 35).

interval between the first and second list, the more those processes that induce and strengthen the associations of the first list will have subsided at the time when the second list is being read and accordingly, the lesser . . . will be the disrupting effect of reading the second list upon these processes. (p. 184)

Retroactive Inhibition by Unrelated Material

To complete their examination of retroactive inhibition, Müller and Pilzecker asked whether the material used to suppress perseveration had to be similar to the learned material (experiment 35). To answer this question, list A was read eight times and immediately followed by the sequential presentation of three pictures showing landscapes (Fig. 3). Subjects were asked to describe each picture for a total of 6 min, after which retention for list A was tested. A control list (list B) was tested for retention after 6 min without intermittent distraction. Again, retention of list A was lower than retention of list B (24% vs. 56%), suggesting that mental activity unrelated to the learned material itself could be disruptive.

Summarizing these results, Müller and Pilzecker reached the following conclusion:

After all this, there is no alternative but to assume that after reading a list of syllables certain physiological processes, which serve to strengthen the associations induced during reading of that list, continue with decreasing intensity for a period of time. These processes and their facilitating effects on these associations are being weakened to a greater or lesser extent if

the experimental subject experiences further mental exertion immediately after reading a list. . . .

It seems justified to suppose that the physiological processes mentioned here are the same that underlie perseverative tendencies. . . . Mental exertion in an experimental subject after reading a list of syllables has firstly the direct effect of weakening the perseverative tendencies of these syllables and secondly, because the effect of these perseverative tendencies is to consolidate syllable associations, the additional effect of impairing these associations. It is the same, quickly fading perseverative tendency that is responsible for the fact that, within about 10 minutes after reading a list of syllables, the recall latency is shorter the earlier testing is done; and the impairment of [the perseverative tendency] . . . handicaps the associations of a list of syllables within the first 10 minutes of reading the list (pp. 196–197).

This conclusion implies that memory is consolidated with a time course of ~10 min. Yet it should be noted that the longest interval between original learning and interpolated activity that Müller and Pilzecker studied was 6 min and that retroactive inhibition was not detected at intervals longer than 1 min. Müller and Pilzecker's value of 10 min seems to have been an estimate drawn from the observed time course of perseveration (see Fig. 1).

McDougall (1901) and Burnham (1903) immediately recognized that perseveration theory provided a way to understand the temporally graded retrograde amnesia (i.e., the loss of premorbid memory) that results from traumatic head injury. Systematic laboratory studies of retrograde amnesia using electroconvulsive shock (ECS) in rats were pioneered by Carl Duncan and generally supported the estimates of Müller and Pilzecker for the time course of consolidation. In these experiments, temporally graded retrograde amnesia for an active avoidance task was produced by ECS up to 15 min following learning but not at intervals longer than 1 hr (Duncan 1949). Duncan's experiments ushered in decades of work in many laboratories to define the time course of memory consolidation by studying ECS-induced retrograde amnesia. The data from these experiments, however, did not converge on a single time course that might have helped to identify the mechanisms underlying memory consolidation. Instead, the time course of memory consolidation appeared to vary widely depending on task parameters (for reviews, see Chorover 1976; McGaugh and Gold 1976).

Although the concepts of perseveration and memory consolidation remained central to the study of learning and memory (for reviews, see Glickman 1961; McGaugh and Herz 1972; Weingartner and Parker 1984), they would eventually be replaced by interference theory as an explanation for retroactive inhibition. Interference theory proposed that memories acquired close together in time compete for representational space, thereby interfering with each other. This theory readily accounted for the original observation of Müller and Pilzecker of a time-dependent disruption of original learning by interpolated material, and could also account for later findings, such as the fact that the degree of disruption increases with greater similarity between interpolated and original

material (for reviews, see McGeoch and Irion 1952; Keppel 1984).⁴ Thus, the perseveration theory of Müller and Pilzecker of memory consolidation fell out of favor within experimental psychology; however, their concepts eventually found considerable utility in biologically oriented studies of memory.

In 1949, in the light of emerging physiological data, Donald Hebb (1904–1985) advanced the dual-trace theory of memory formation. This theory revived the idea of perseveration by postulating a short-term memory in the form of reverberatory activity within local neural circuits. Reverberation was proposed to induce structural changes at synapses in the reverberating network and thus permit the memory to be stored more permanently (Hebb 1949). Hebb's ideas marked a shift in the approach to memory consolidation from manipulating memory in intact animals to studying the biological events that underlie the phenomenon of consolidation. For example, the postulate of structural change suggested a role for protein synthesis in the fixing of memory, which was confirmed by experiment (Flexner et al. 1963; Agranoff and Klinger 1964; Barondes and Cohen 1965; for review, see Davis and Squire 1984). Today, it is thought that the phenomenon of memory consolidation in the minutes and hours after learning depends, in part, on a cascade of molecular events that lead to changes in the properties of neurons (e.g., Bailey and Chen 1983; Goelet et al. 1986; Alberini et al. 1994; O'Leary et al. 1995; Tully et al. 1995; Dudai 1996). These events include activation by second messenger cascades of transcriptional regulators, and multiple waves of mRNA and protein synthesis. Some of the proteins produce functional changes in neurons and synapses, whereas others lead to structural changes. In this sense, the ideas of Müller and Pilzecker can be traced from their origin to contemporary studies of the neuronal events that occur during a brief time period, shortly after learning.

Yet the term consolidation is also used today in the context of observations that memory can remain vulnerable to some manipulations for weeks, months, and even years after learning. In 1957, Scoville and Milner described severe anterograde and temporally limited retrograde amnesia following bilateral removal of medial temporal lobe structures. This finding led ultimately to the identification of the hippocampus and adjacent anatomically related cortical structures of the medial temporal lobe as components of a memory system that is essential for the formation of long-term memory (Squire and Zola-Morgan 1991). Disrupting the function of this system causes retrograde amnesia, which is most severe for recent events and gradually less severe for remote events. Graded retrograde amnesia can extend across several years in humans (Russell and Nathan 1946; Squire et al. 1975) and across weeks in mice (Squire and Spanis 1984; for review, see Milner et al. 1998). Together, these findings suggest that medial temporal lobe structures contribute to the prolonged and gradual consolidation of memory over the course of weeks or even years. Specifically, the

⁴Müller and Pilzecker themselves proposed an interference theory based on several experiments in which a cue syllable was trained with two different associates. These experiments showed that two associations with the same cue syllable were less well remembered than a single association. Müller and Pilzecker interpreted these findings as evidence for a competitive interference between the alternative syllables during acquisition and/or retrieval (see Appendix).

hippocampus has been proposed to direct a gradual process of reorganization and stabilization of representations in the neocortex (for reviews, see Squire and Alvarez 1995; Knowlton and Fanselow 1998). Although this process is likely to involve changes at synapses, it depends fundamentally on the successful interaction between the hippocampus and the neocortex and is distinct from the process by which synaptic efficacy is altered during the early phases of memory formation.

Müller and Pilzecker's perseveration theory of memory consolidation was the starting point for discoveries of molecular and cellular events and brain systems important for memory formation. The neuronal events and processes that occur at the level of brain systems may unfold across different time scales, but all contribute to the dynamic and selective process of fixing memory over time. A challenge remaining for the next century is to understand, in detail, all the processes that underlie the phenomenon of memory consolidation—molecular and cellular events at synapses, the operations of brain systems, and the interactions among them.

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Appendix

SYLLABLE LISTS

Typical lists consisted of 12 nonsense syllables (6 pairs), printed in a single column on a strip of paper, and mounted on a rotating drum. The

rotation speed of the drum could be adjusted to match the reading speed of each subject (e.g., 12 syllables in 8 sec). Each syllable was composed of two consonants separated by a vowel sound. Lists were constructed such that the initial and final consonants within a list, as well as the middle sounds, were unique (except when the number of syllables exceeded the number of possible consonants and vowel sounds). In addition, the final consonant of a syllable was always different from the first consonant of the next syllable, and adjacent syllables could not form a word. Finally, syllables that were difficult to pronounce were discarded, resulting in a total pool of 2210 syllables. The syllables were written on cards and drawn by lot, taking precautions not to use a syllable twice within 14 days.

TESTING APPARATUS

To measure retention of paired associates, the emphasized syllables of a previously studied list were mounted on a rotating drum, which was hidden behind a window that could be opened and closed to control the display. The window was held closed by an electromagnet and could be opened by a switch that was controlled by the experimenter. A chronometer was triggered by opening the window. The chronometer was stopped automatically when the experimental subject produced a syllable, because the response would be registered by either a vibration-sensitive device or a lever that was displaced by lip movements. After the subject had responded to the cue syllable, the window was closed and the drum advanced to the next cue. This device could measure changes in response latency with an accuracy on the order of a few milliseconds.

SUBJECTS AND INSTRUCTIONS

The 40 experiments reported by Müller and Pilzecker were carried out with a small group of students, colleagues, and relatives. Each experiment involved a single subject, who typically participated in 24 days of training and testing. Nearly half of the experiments ($n = 19$) were carried out with Müller's and Pilzecker's spouses. For another three experiments, Müller and Pilzecker themselves served as experimental subjects. Experimental subjects were instructed to read each syllable of a list aloud and not to rehearse lists during retention intervals. In the early experiments, subjects were offered reading material to help suppress any spontaneous tendency to rehearse previously trained lists (perseveration) during retention intervals. Later, as evidence for retroactive inhibition emerged, this practice was abandoned. During the test, subjects were asked to name the syllable that was associated with the cue as quickly as possible. They were not required to be certain that their answer was correct, but to indicate those cases in which they could not reproduce any associate with confidence. Although subjects were allowed to correct their answers, the latency and accuracy of the first answer were scored.

REMAINING EXPERIMENTS

This commentary focuses on only 10 of the 40 experiments reported by Müller and Pilzecker. A brief description of all the experiments is presented here.

EXPERIMENTS 1-6

Parametric studies of the effects of repetition and retention interval on cued recall performance. A lawful relationship was found between the number of training trials, retention interval, percentage of correct recall,

and recall latency. Increasing the number of training trials led to better recall (consistent with Ebbinghaus' results) and recall latency correlated with the length of the retention interval.

EXPERIMENTS 7-27

Parametric studies of interference between associations, which was produced by first presenting a pair of syllables (e.g., "ser-lad") and later using the cue syllable of that pair in the training of another association (e.g., "ser-kum"). Recall was consistently lower for the ambiguous cues (e.g., "ser") than for unambiguous control syllables.

EXPERIMENTS 28-37

Studies of retroactive inhibition (see text).

EXPERIMENTS 38-40

Studies demonstrating that the particular metric style used to read the syllables during training influenced which syllables were associated with each other. Reading the list in trochees, for example, induced the strongest associations between the emphasized and subsequent syllable, whereas other metric styles favored other associations.